Polar Biology
https://doi.org/10.1007/s00300-023-03124-w

ORIGINAL PAPER

Concentration of different forms of phosphorus in soils affected by the little auk (*Alle alle*) and their relationship with tundra vegetation in Spitsbergen (Svalbard, High Arctic)

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Received: 24 October 2022 / Revised: 7 February 2023 / Accepted: 17 March 2023
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Abstract

The purpose of the present study was to determine the link between planktivorous little auks (*Alle alle*) and their soil fertilization, the concentration of total, and different forms of phosphorus in the surface layer of the High Arctic soils and the vascular plant composition of the tundra vegetation. Samples of the surface soil layer (0–10 cm) were collected along three pairs of transects (affected and unaffected by little auks) at different locations in Spitsbergen (Svalbard). The surface layer of soils affected by little auks was characterized by a significantly higher mean concentration of Ptot (1.02–1.44 g kg^{-1}) compared to those not affected by seabirds (0.58–0.77 g kg^{-1}). The mean concentration of different forms of P was also generally higher in soils affected by seabirds (i.e., labile P: 0.13–0.34 g kg^{-1}, moderately labile P: 0.31–0.90 g kg^{-1}, stable P: 0.27–0.39 g kg^{-1}) than in unaffected soils (labile P: 0.04–0.18 g kg^{-1}, moderately labile P: 0.30–0.37 g kg^{-1}, stable P: 0.12–0.24 g kg^{-1}); however, the differences were not always significant, most likely due to the high heterogeneity of specific environmental conditions at the local scale such as soil type, soil chemical composition, and vegetation type. Vascular plant cover was significantly and positively related to the concentration of the P forms studied in the soil. The phosphorus gradient significantly altered the composition of the vascular plants and explained 58.4% of its variation. Little auks are an important source of soil phosphorus in terrestrial ecosystems in the High Arctic that significantly affect the cover and composition of vascular plants.

Keywords Little auk · *Alle alle* · High Arctic · Phosphorus · Seabirds · Tundra vegetation

Introduction

Soils in the High Arctic are characterized by low availability of nutrients mostly due to very weak chemical weathering, which is responsible for the release of various elements such as calcium (Ca), magnesium (Mg), and potassium (K) from rocks and minerals (Skiba et al. 2002; Kabała and Zapart 2012; Szymański et al. 2015). A very limited natural supply of other nutrients such as nitrogen (N) and phosphorus (P) results from very low wet and dry atmospheric deposition of these elements in the Arctic (Solheim et al. 1996; Gordon et al. 2001; Madan et al. 2007; Skrzypek et al. 2015) as well as a low rate of mineralization of soil organic matter (White et al. 2004; Bradley-Cook and Virginia 2016). However, sites in the Arctic found adjacent to seabird colonies exhibit a much higher supply of nutrients such as N, P, Ca, and K originating from the birds' guano, feathers, eggshells, and other biological waste versus other sites (Godzik 1991;

This article belongs to the special issue on the "Pathways and impacts of biotically-mediated marine and other stored nutrient transfer between polar ecosystems", coordinated by Peter Convey, Katarzyna Zmudczyńska-Skarbek, and Stef Bokhorst.

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Published online: 06 April 2023

Headley 1996; Zwolicki et al. 2013, 2016a, b; Ziółek and Melke 2014; Szymański et al. 2016a, b; González-Bergonzoni et al. 2017; Otero et al. 2018). Thus, seabirds that feed at sea and breed on land represent a crucial natural factor responsible for the transport of organic and inorganic matter from marine to terrestrial ecosystems, which in turn strongly affects the chemical properties of soils and tundra vegetation (Zwolicki et al. 2013, 2016a, b; Szymański et al. 2016a, b; Szymański 2017a, b) as well as soil and limnoterrestrial invertebrate communities (Zmudczyńska-Skarbek et al. 2015, 2017; Zawierucha et al. 2016).

Among nutrients important for terrestrial ecosystems, which are mostly deposited on land by seabirds, is phosphorus (Zwolicki et al. 2013; Otero et al. 2015, 2018; Szymański et al. 2016b; De La Peña-Lastra 2021; Finne et al. 2022). It is responsible for plant growth and vegetation cover development because it affects essential biochemical and physiological processes in plants including uptake, transport, and assimilation of other nutrients (Brady and Weil 2004; Condron and Newman 2011). In addition, P plays a crucial role in photosynthesis, N fixation, and root development (Gordon et al. 2001; Brady and Weil 2004; Condron and Newman 2011; Ziółek and Melke 2014). Deficiency of P in soil limits primary production while its excess is often responsible for undesired eutrophication of ecosystems (Elser et al. 2007; Madan et al. 2007; Breuning-Madsen et al. 2008).

Phosphorus in soils and sediments may occur in various organic and inorganic forms and therefore exhibits different availability to plants. In addition, it has been shown that total phosphorus content in soil is not a reliable predictor of P availability to plants in tundra and forest ecosystems (Jonasson et al. 1993; Niederberger et al. 2017, 2019). Thus, sequential fractionation of P is needed, which allows to determine the content of readily available forms of P to plants (so-called labile P) as well as more immobilized forms of P that are either less available (moderately labile P) or even not available (stable P) to plants (Niederberger et al. 2017, 2019). Among several protocols of sequential extraction of P employed in the last few decades (Chang and Jackson 1957; Hieltjes and Lijklema 1980; Hedley 1982a; Ruttenberg 1992), the most widely used, reliable, and also most applicable to studies conducted in areas poor in nutrients is the method given by Hedley (Hedley et al. 1982a, b; Tiessen and Moir 1993; Cross and Schlesinger 1995; Hinsinger 2001; Condron and Newman 2011; Vincent et al. 2014; Niederberger et al. 2017).

Numerous ecological studies describe the importance of planktivorous seabirds for Arctic terrestrial ecosystems in soil fertilization via nutrients containing guano as well as distribution of N and P in tundra ecosystem (Zmudczyńska et al. 2012; Zmudczyńska-Skarbek et al. 2013; Zwolicki et al. 2013, 2016a, b; Wojciechowska et al. 2015; Szymański et al. 2016a, b; González-Bergonzoni et al. 2017); however, a relationship between nutrient delivery by seabirds, concentration of different phosphorus forms in the soil, and their relationship to vegetation growth has not been shown. Therefore, the results of our study are important for a better understanding of the close relationship between guano deposition, fertility of soils (availability of P), plant diversity, and productivity of tundra vegetation in such areas.

The main aims of this study were (1) to determine the importance of little auks (*Alle alle*) for the concentration of different forms of phosphorus in the surface soil layer of a terrestrial High Arctic ecosystem in Spitsbergen (Svalbard), and (2) to determine the relationship between different soil P forms, vegetation cover, and plant species composition. We hypothesize that seabird-related soil fertilization significantly increases the concentration of all of the studied phosphorus forms in the soil; however, only the labile form of P, which is the most available to plants, is responsible for a substantial change in tundra vegetation and affects the composition of plant species.

Materials and methods

Study area

The study was carried out in the vicinity of little auk colonies at three different locations in Spitsbergen (Svalbard), i.e., on the northern coast of Magdalenefjorden (Høystakken Mt., NW Spitsbergen), southern coast of Isfjorden (Platåberget Mt., central Spitsbergen), and northern coast of Hornsund (Ariekammen Mt., SW Spitsbergen) (Fig. 1). The little auk colonies in Magdalenefjorden, Hornsund, and Isfjorden consisted of 18,000, 23,500, and 250 breeding pairs, respectively (Zwolicki et al. 2016b). In terms of geology, old crystalline rocks such as gneiss, migmatite, and granite prevail in the Magdalenefjorden area (Elvevold et al. 2007). The Hornsund area is characterized by the occurrence of old crystalline metamorphic rocks including schist, paragneiss, quartzite, amphibolite, and marble (Czerny et al. 1993; Majka et al. 2010). On the other hand, sedimentary, clastic rocks such as sandstone, mudstone, and shale from the Paleocene and Eocene occur in the Isfjorden area (Dallman et al. 2001). Leptic Regosols and Skeletic Regosols occur on slopes with seabird colonies in each location. Coastal plains in the Hornsund and Magdalenefjorden areas as well as in Bjørndalen (Isfjorden area) are characterized by occurrence of Haplic Cryosols and Turbic Cryosols (IUSS Working Group WRB 2022). Magdalenefjorden is impacted by warm Atlantic water masses carried by the West Spitsbergen Current flowing from the south with a periodic influx of cold waters from the north (Zwolicki et al. 2016b). Hornsund is impacted by the cold Sørkapp Current carrying Arctic water masses

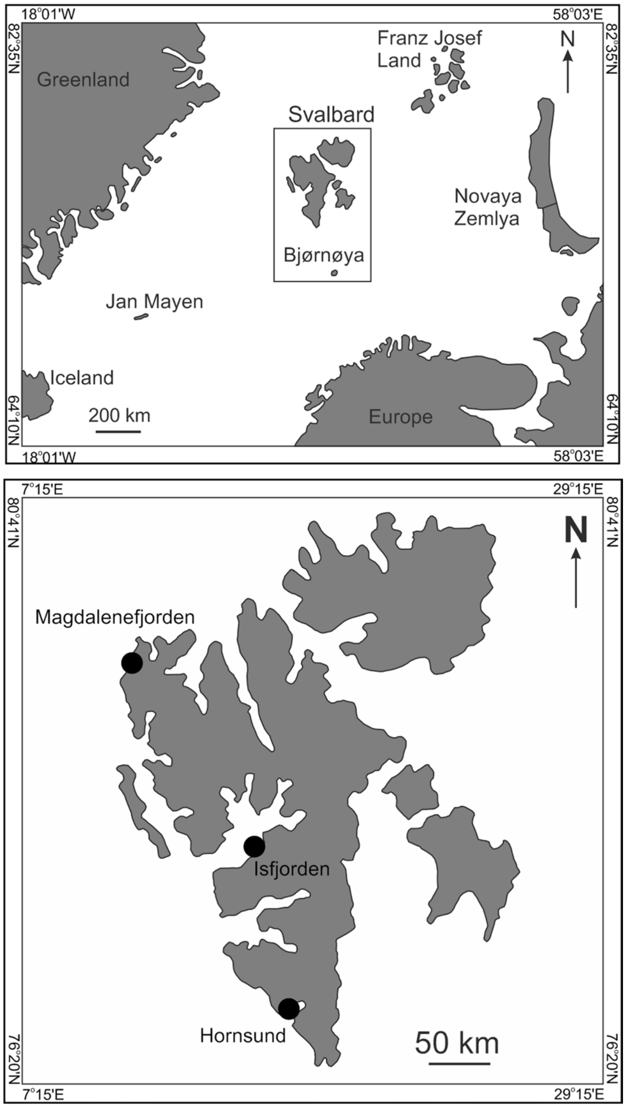


Fig. 1 Location of the study area

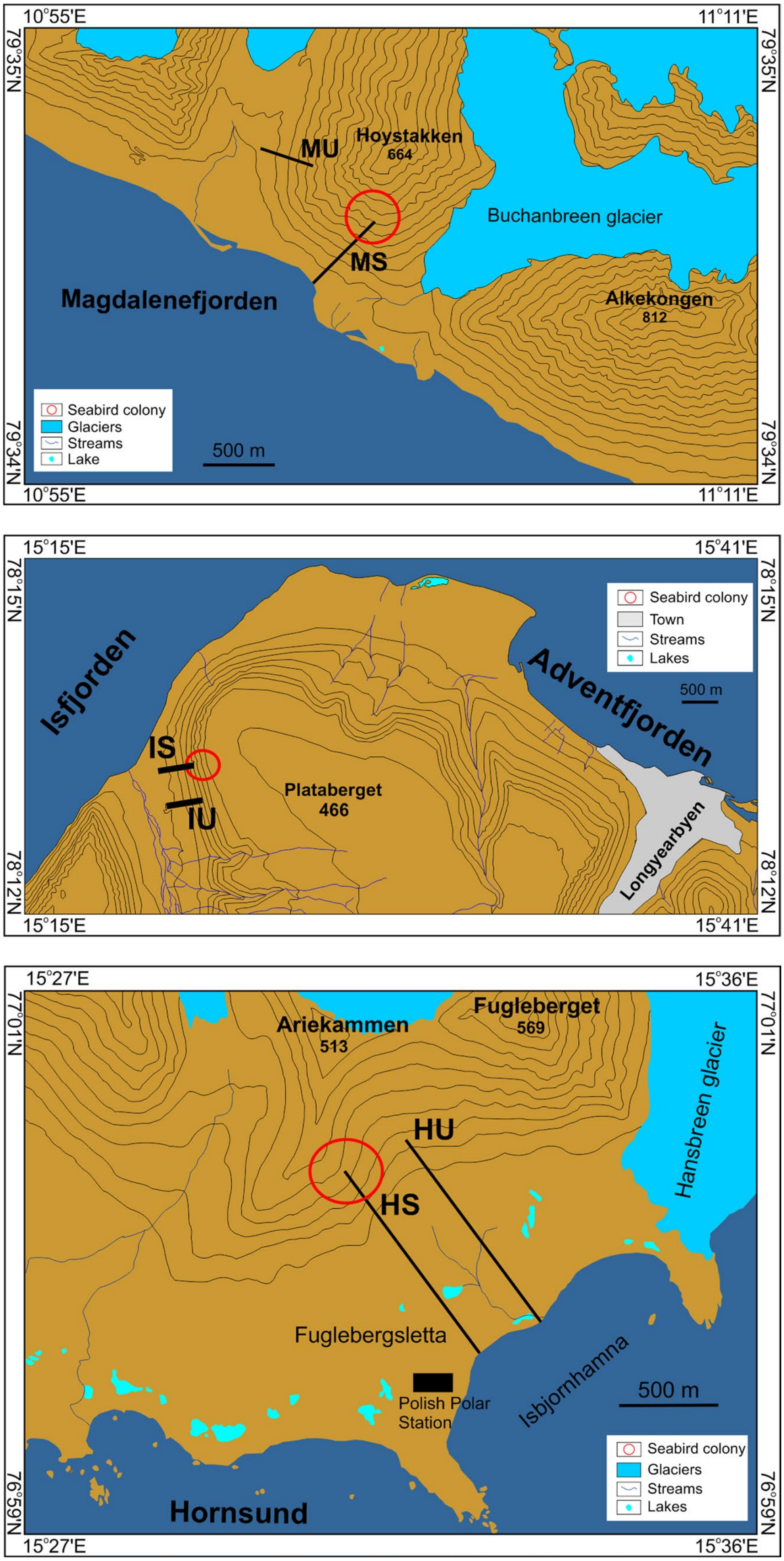
from the northwestern part of the Barents Sea with occasional inflows of warmer Atlantic waters from the West Spitsbergen Current (Zwolicki et al. 2016b). Mean annual air temperature (MAAT) in Hornsund is – 4.2 °C and total annual precipitation is 450 mm (Marsz and Styszyńska 2007; Marsz 2013). The Isfjorden area is characterized by the strongest impact of warmer Atlantic waters from the West Spitsbergen Current from all the studied areas. Therefore, this study area is the warmest and driest. The mean annual air temperature and total annual precipitation in this area are—2.6 °C (mean from the period 2005–2017) and 192 mm, respectively (Matsuoka et al. 2018). The Magdalenefjorden and Hornsund areas are characterized by northern Arctic tundra with dwarf-shrub and herb species of subzone B, whereas the Isfjorden area is characterized by middle Arctic tundra with prostrate and hemiprostrate dwarf-shrub species of subzone C (Jónsdóttir 2005; Johansen et al. 2012; Johansen and Tømmervik 2014).

Field and laboratory methods

Samples of the surface soil layer (uppermost 10 cm) were collected along three pairs of transects established at each location described above. The transect approach was used because we assumed that in the terrestrial ecosystem of the High Arctic, which is poor in nutrients such as nitrogen and phosphorus (e.g., Cocks et al. 1999; Stempniewicz 2005; Bokhorst et al. 2007; Zwolicki et al. 2013, 2016b), the distance from the seabird colony is the main reason affecting the concentration of total P and different forms of P in the soil (Ziółek and Melke 2014; Szymański et al. 2016b). One of the transects from each pair ran from the studied seabird colony to the seashore, while the second was established at a topographically similar location, but not under the routine flight path of the studied seabirds, thus experiencing either no impact or only negligible ornithogenic impact (Fig. 2). Along each transect, depending on the distance from the seabird colony to the seacoast, 8 to 12 sampling plots (160 × 160 cm each) were established. The first plot was located in the center of the colony, while subsequent plots were located at an increasing distance from each transect starting point (plot 1) as follows: plot 2 (6 m), 3 (15 m), 4 (29 m), 5 (49 m), 6 (79 m), 7 (125 m), 8 (193 m), 9 (296 m), 10 (449 m), 11 (680 m), and 12 (1026 m) (Zwolicki et al. 2013, 2016a, b). Three soil samples from each study plot were collected. Two of them were collected from diagonal corners of the plot, and the third sample was collected from the center of the plot.

The soil samples collected were air dried, then gently crushed, and sieved through a 2-mm sieve in the laboratory. All soil analyses were performed using all collected soil samples (i.e., three soil samples per plot), and then the results were averaged to obtain one value per plot. Soil pH was measured in distilled water in 1:2 v/v ratio (Thomas 1996). Total carbon (TC) and total nitrogen (TN) in the studied soils were determined using a CHN elemental analyzer (Thermo Fisher, Flash EA 1112) in triplicate and then averaged. Prior to the analysis, the soil samples were homogenized by grinding them in a mortar. Total carbon content was assumed to be total organic carbon (TOC), as all the studied soils did not contain carbonates (no reaction was observed after 10% HCl treatment of soil samples). In order to assess the nitrogen isotopic signature (δ^{15}N) in the soil, samples were sieved (0.25 mm mesh) to remove coarse material and subsequently ground using a vibrating mill (LMW-S, Testchem) to a grain size of less than 0.03 mm. The nitrogen isotope ratio was determined using a continuous flow mass spectrometer (Thermo Fisher, Delta V Advantage) coupled with an elemental analyzer (Thermo

Fig. 2 Detailed location of the studied seabird-affected (MS, IS, HS) and unaffected (MU, IU, HU) transects



Fisher, Flash EA 1112). All samples with stable isotopes were analyzed in a laboratory at the University of La Rochelle (France). The results were expressed using conventional $\delta^{15}N$ notation, according to the following equation:

$$\delta X = \left(R_{\text{sample}} R_{\text{standard}}^{-1} - 1\right) 1.000(‰), \quad (1)$$

where R_{sample} is the stable isotope ratio $^{15}N/^{14}N$ in the analyzed sample, and R_{standard} is the stable isotope ratio $^{15}N/^{14}N$ in reference atmospheric N_2 (Kelly 2000).

Fractionation of the phosphorus forms in the studied soils was conducted using the Hedley method (Hedley 1982a) using the modification by Tiessen and Moir (1993). For this analysis 0.5 g of soil sample was used, in which the phosphorus forms were sequentially extracted using a series of reagents of different chemical strength (soil/solution ratio 1:100). However, the samples were first ground in a mortar in order to homogenize the material and to obtain a very fine powder. Readily-soluble phosphorus forms (i.e., labile P–Pl) were then extracted with distilled water (soluble P–P H_2O) as well as 0.5 M $NaHCO_3$ (i.e., readily decomposable organic P and exchangeable mineral P–P HCO_3), followed by moderately available phosphorus forms (i.e., moderately labile P–Pml), which were extracted using 0.1 M NaOH (i.e., mineral P bound to Al and Fe oxides and organic P in organic acids–P NaOH) and 1 M HCl (i.e., mineral P bound to calcium–P HCl). The most stable phosphorus form (i.e., stable P–Pst) was extracted using 12 M HCl with heating (i.e., poorly soluble mineral and organic P–P HClconc) and finally occluded, insoluble phosphorus bound to primary or secondary minerals using 65% HNO_3 and H_2O_2 (P residual). Total phosphorus (Ptot) was calculated as the sum of the fractions extracted via the modified Hedley method (Simas et al. 2007; Giesler et al. 2012). We did not separate inorganic P from organic P, especially in the case of NaOH extracts and labile and moderately labile fractions because of rapid changes between the mineral and organic soil P forms (Henríquez and Killorn 2005; Niederberger et al. 2019). The content of each given phosphorus fraction was determined spectrophotometrically using SPECORD 50 (Analytik Jena) via the chlorostannous acid method (Kuo 1996).

Vascular plant species were identified for each sampling plot from which the soil samples were collected and the percentage share of individual species was visually estimated. Moreover, the total share of vegetation cover as well as vascular plant and cryptogam cover were visually assessed for each of the study plots established along each studied seabird-affected and unaffected transect.

Statistical analysis

The importance of seabird impact on phosphorus form concentration was examined using redundancy analysis (RDA), while related changes in plant composition were calculated using canonical correspondence analysis (CCA). The unimodal or linear method was selected based on data structure using gradient length. In both direct ordination techniques used in the study, the hypotheses were tested using the Monte Carlo permutation test (999 permutation). For multiple comparisons, we used Holm's (1979) correction to control familywise type I errors. We used one axis in the case of RDA and three axes in the case of CCA to compare them with corresponding unconstrained models (PCA or DCA, respectively). This way efficiency values [%] for each model/variable were calculated (ter Braak and Šmilauer 2012). Because of data skewness, all dependent variables were logarithmically transformed $y = \log(x + 1)$. In order to find significant relationships between plant species and Pl as well as Pml, a *t*-value biplot (with Van Dobben circles), which approximates the *t*-values of regression coefficients of a weighted multiple regression, was created (ter Braak and Šmilauer 2012). In order to explore the various relationships between different soil phosphorus forms and soil $\delta^{15}N$, and plant species responses to those phosphorus forms, we employed Generalized Additive Models (GAMs), while the Akaike Information Criterion (AIC) was used to find the best fit (ter Braak and Šmilauer 2012).

Differences in mean Ptot content and the amount of the studied forms of P in the surface soil layer between the three studied seabird transects and three unaffected transects separately at each location were evaluated by using the nonparametric Mann–Whitney *U*-test (level of significance at $p < 0.05$). Relationships between different forms of P and some soil chemical properties (i.e., pH, $\delta^{15}N$, TOC, and TN content) in all the studied transects combined were determined using Spearman's rank correlation coefficient (r_S). This correlation coefficient (r_S) was also calculated for each of the studied P forms and total share of tundra vegetation, vascular plant cover, and cryptogam cover for all of the studied transects combined. Relationships between concentration of Ptot and the studied forms of P with distance from the center of the seabird colony separately for each location were calculated using Pearson correlation coefficient (r). All statistical calculations were performed using Statistica 13 software (StatSoft, Tulsa, OK, USA).

Results

Concentration of total phosphorus and different forms of phosphorus in the soil

The mean concentration of Ptot and different forms of P in the surface soil layer in the studied seabird-affected and unaffected transects is presented in Table 1, while the concentration of P originating from each extraction is presented in the Online Resource 1, Table S1. The mean

Table 1 Mean concentration of different forms of phosphorus (P) in surface soil layer along the studied transects

Transect	*n*	Pl[a] ($g\ kg^{-1}$)	Pml[b]	Pst[c]	Ptot[d]
Hornsund					
Seabird-affected	12	0.20 (0.01)a	0.90 (0.11)a	0.33 (0.05)a	1.44 (0.14)a
Unaffected	11	0.18 (0.01)a	0.30 (0.01)b	0.12 (0.02)b	0.60 (0.02)b
Magdalenefjorden					
Seabird-affected	9	0.34 (0.04)a	0.31 (0.03)a	0.39 (0.11)a	1.04 (0.13)a
Unaffected	8	0.16 (0.01)b	0.37 (0.02)a	0.24 (0.02)a	0.77 (0.02)b
Isfjorden					
Seabird-affected	9	0.13 (0.01)a	0.63 (0.05)a	0.27 (0.05)a	1.02 (0.07)a
Unaffected	9	0.04 (0.01)b	0.32 (0.02)b	0.21 (0.04)a	0.58 (0.04)b

Values in parentheses are standard errors. For a given column, significant difference (at $p < 0.05$) in mean value between particular seabird-affected transect and its respective unaffected transect is marked with different letters based on the Mann–Whitney U-test

[a] Labile P

[b] Moderately labile P

[c] Stable P

[d] Total P

concentration of Ptot was always significantly higher in the soil located along the seabird-affected transects compared to the soil occurring along the unaffected transects (Table 1). Among the studied seabird-affected transects, the highest mean Ptot concentration was observed in soils of Hornsund area (1.44 $g\ kg^{-1}$) and the lowest mean Ptot concentration was obtained for soils of Isfjorden area (i.e., 1.02 $g\ kg^{-1}$) (Table 1). The mean concentration of Ptot in the studied soils located along unaffected transects was the highest in the Magdalenefjorden area (0.77 $g\ kg^{-1}$) and the lowest in the soils of the Isfjorden area (0.58 $g\ kg^{-1}$) (Table 1).

The mean concentration of Pl in the soils that occurred along the seabird-affected transect was significantly higher than the mean concentration of Pl in the soils located along the unaffected transect in the Magdalenefjorden and Isfjorden areas (Table 1). Among the studied seabird-affected transects, the highest mean Pl concentration was obtained for soils in the Magdalenefjorden area (0.34 $g\ kg^{-1}$) and the lowest in the Isfjorden area (0.13 $g\ kg^{-1}$) (Table 1). The soils that occurred along the unaffected transect in Hornsund area exhibited the highest mean concentration of Pl (i.e., 0.18 $g\ kg^{-1}$) and the soils along the unaffected transect in the Isfjorden area were characterized by the lowest mean concentration of Pl (0.04 $g\ kg^{-1}$) among all unaffected transects studied (Table 1).

The mean concentration of Pml in the soils of the seabird-affected transect was significantly higher than the concentration of Pml in the soils of the unaffected transect in the Hornsund and Isfjorden areas. Among the studied seabird-affected transects, the highest mean Pml concentration in the soils was observed in the Hornsund area (0.90 $g\ kg^{-1}$) and the lowest mean Pml concentration was obtained for the soils in the Magdalenefjorden area (0.31 $g\ kg^{-1}$). The mean concentration of Pml in the soils occurring along the unaffected transects was very similar in each of the locations studied (0.30–0.37 $g\ kg^{-1}$) (Table 1).

The mean concentration of Pst was higher in soils from seabird-affected transects than in soils occurring along unaffected transects. However, the difference between the mean concentration of Pst in the soils studied along the seabird-affected and unaffected transects was significant only in the case of the Hornsund area. Among the studied seabird-affected transects, the highest mean Pst concentration in soils was obtained in the Magdalenefjorden area (0.39 $g\ kg^{-1}$) and the lowest in the Isfjorden area (0.27 $g\ kg^{-1}$) (Table 1). The highest mean Pst concentration was obtained in the soils of the unaffected transects studied in the Magdalenefjorden area (0.24 $g\ kg^{-1}$) and the lowest in the Hornsund area (0.12 $g\ kg^{-1}$) (Table 1).

Relation between concentration of total phosphorus and different forms of phosphorus in the soil with distance from the seabird colony

The concentration of Ptot and the studied P forms in the surface soil layer along the studied seabird-affected and unaffected transects is presented in Figs. 3 and 4. The concentration of Ptot in the soil clearly decreased with increasing distance from the seabird colony in the case of the Hornsund and Magdalenefjorden areas (Fig. 3a–b). However, in the case of Magdalenefjorden area, the highest concentration of Ptot was observed in the soil (1.61 $g\ kg^{-1}$) about 50 m from the center of the seabird colony. The concentration of Ptot in the soil did not change clearly along the seabird-affected

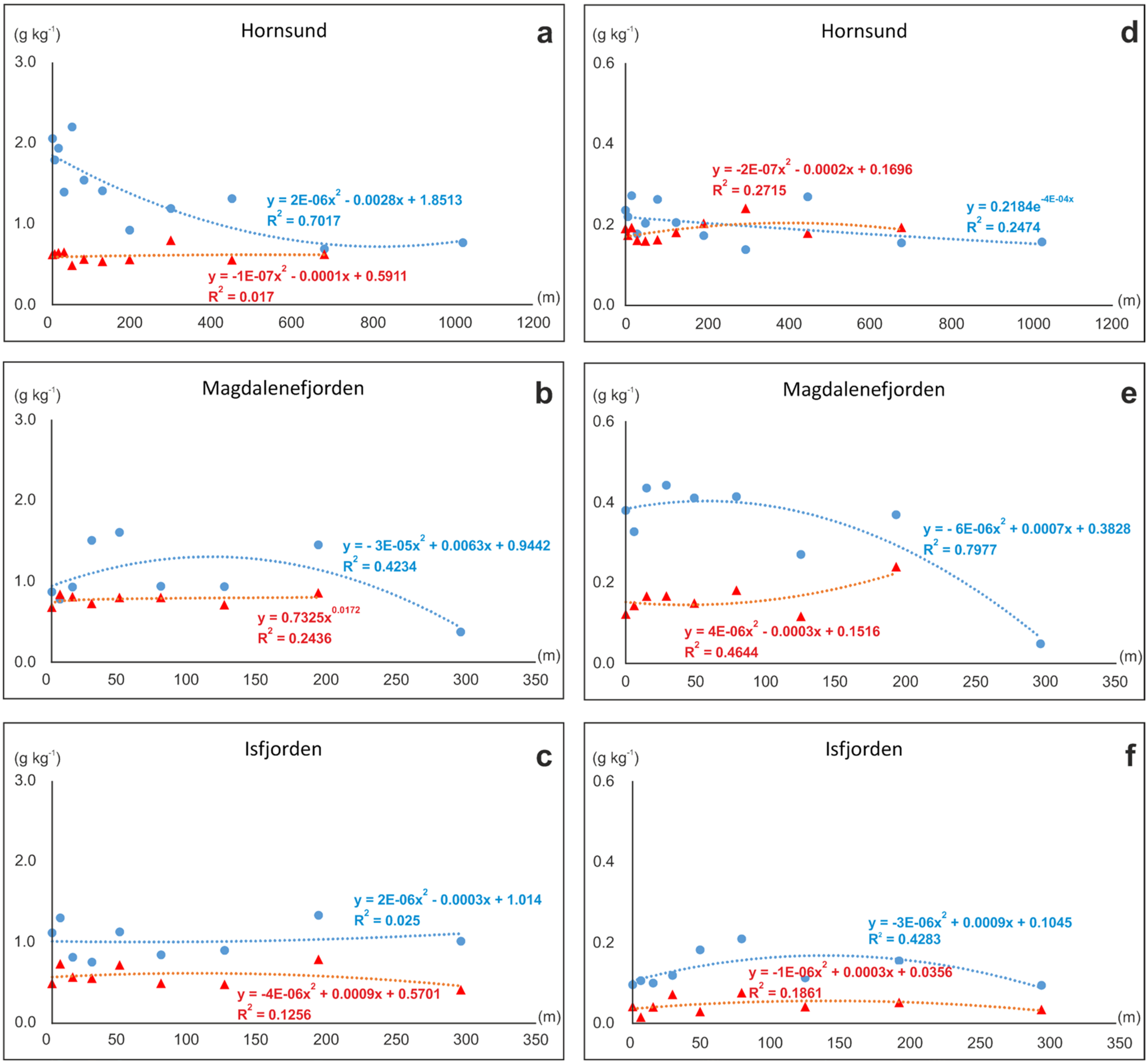


Fig. 3 Total phosphorus (**a-c**) and labile phosphorus form (**d-f**) concentration in soils along the studied seabird-affected transects (blue circles) and unaffected transects (red triangles)

transect in the Isfjorden area (Fig. 3c) as was the case for all the unaffected transects studied (Fig. 3a–c).

The concentration of Pl in the soil decreased with increasing distance from the seabird colony in the case of the Hornsund and Magdalenefjorden areas (Fig. 3d–e). In the case of the seabird-affected transect in the Isfjorden area and all the studied unaffected transects, the concentration of Pl did not change clearly or increased (in the case of the unaffected transect in the Magdalenefjorden area) along the transects (Fig. 3d–f).

The concentration of Pml in the soil along the seabird-affected transect from Hornsund and Magdalenefjorden areas decreased with increasing distance from the seabird colony (Fig. 4a–b). On the other hand, Pml concentration increased along the seabird-affected transect in the Isfjorden area (Fig. 4c). The concentration of Pml did not change clearly along all the studied unaffected transects (Fig. 4a–c).

The concentration of Pst in the studied seabird-affected transects decreased (Hornsund, Isfjorden) or increased (Magdalenefjorden) along the transects (Fig. 4d–f). The concentration of Pst did not change clearly along all the studied unaffected transects (Fig. 4d–f).

The Pearson correlation coefficients between the concentration of Ptot and the forms of P studied with the

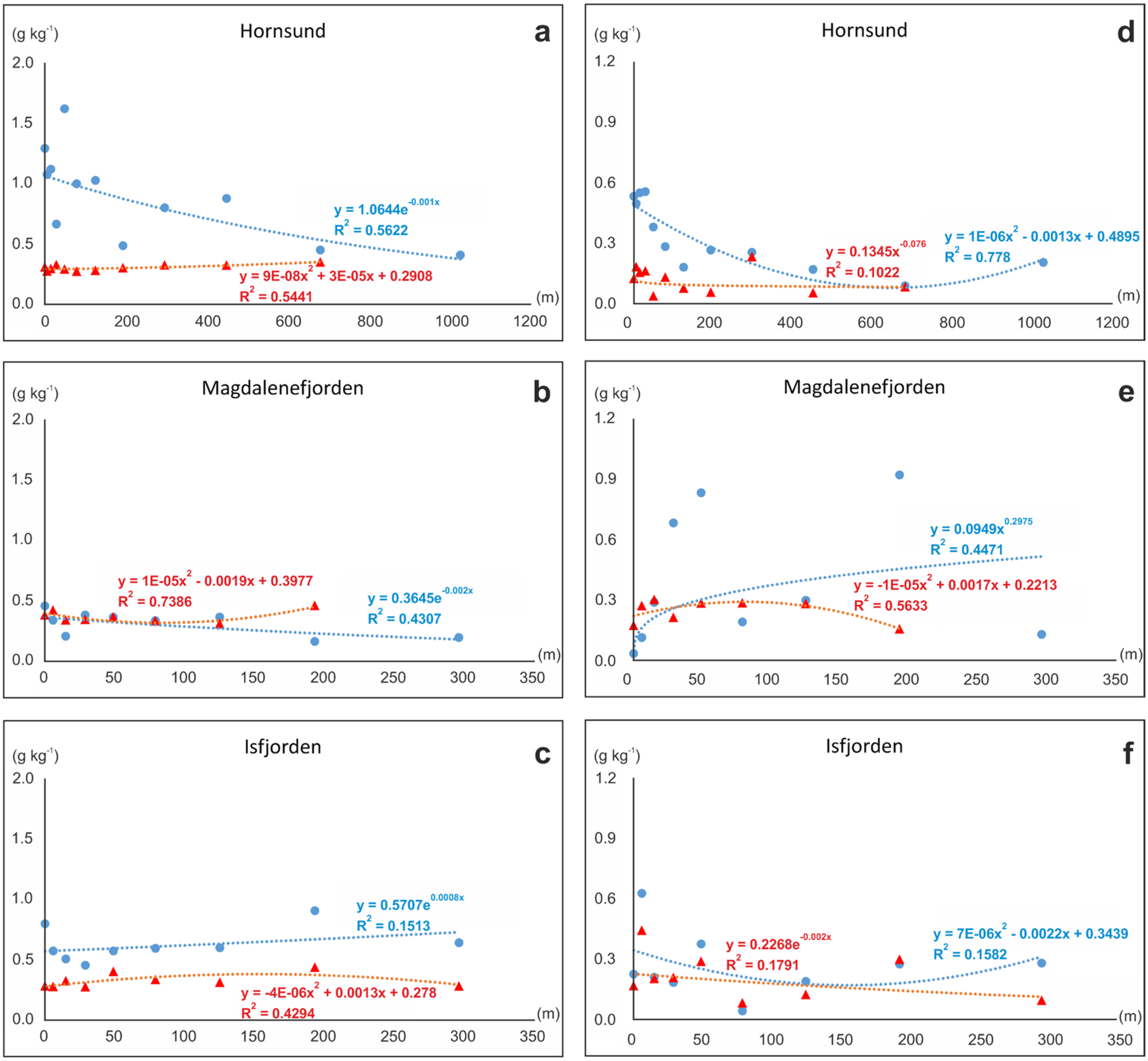


Fig. 4 Moderately labile phosphorus form (**a**–**c**) and stable phosphorus form (**d**–**f**) concentration in soils along the studied seabird-affected transects (blue circles) and unaffected transects (red triangles)

distance from the center of the seabird colony are presented in Table 2. Total phosphorus and all studied forms of P exhibited a negative correlation with the distance from the center of the colony in the Hornsund area; however, the correlation between Pl concentration and distance was not significant (Table 2). Total phosphorus and all the studied forms of P, with the exception of Pst, also exhibited a negative correlation with distance in the Magdalenefjorden area; however, only the relationship between concentration of Pl and distance was significant (Table 2). In the case of the Isfjorden area, the correlation coefficients obtained between Ptot concentration and different forms of

Table 2 Relation between different forms of phosphorus and distance from the center of the seabird colony

Location	Pl[a]	Pml[b]	Pst[c]	Ptot[d]
Hornsund	−0.47	−0.68*	−0.69*	−0.78*
Magdalenefjorden	−0.80*	−0.65	0.10	−0.32
Isfjorden	−0.01	0.37	−0.14	0.14

*Significant at $p < 0.05$

[a] Labile P

[b] Moderately labile P

[c] Stable P

[d] Total P

P and distance from the center of the seabird colony were not significant (Table 2).

Relationships between different forms of P in the soil and chemical properties of the soil

The concentrations of Pl, Pml, Pst, and Ptot observed in the soils of all the studied seabird-affected and unaffected transects combined were significantly and positively correlated with the content of TOC and TN in the soil (Table 3). Pst and Ptot concentrations in these soils were also significantly and negatively correlated with soil pH (Table 3).

The gradient of soil $\delta^{15}N$ significantly affected the concentration of three forms of P in the soil (RDA, pseudo-$F=20.3$, $p=0.001$) and explained the majority of its non-random variation (efficiency = 55.7%; Fig. 5a). The three forms of P were significantly and positively correlated with $\delta^{15}N$; however, the Pml form exhibited a nonlinear response with a faster increase toward higher $\delta^{15}N$ values (Table 3; Fig. 5b).

Table 3 Spearman's rank correlation coefficients between different forms of phosphorus and chemical properties of soils in the studied transects combined

Soil property	Pl[a]	Pml[b]	Pst[c]	Ptot[d]
pH	−0.176	−0.222	−0.352*	−0.408*
$\delta^{15}N$	0.592*	0.504*	0.481*	0.756*
TN	0.605*	0.379*	0.324*	0.603*
TOC	0.594*	0.329*	0.280*	0.561*

*Significant at $p < 0.05$

[a] Labile P

[b] Moderately labile P

[c] Stable P

[d] Total P

Relationships between different forms of P in the soil and the composition of the plant community

Table 4 lists the Spearman rank correlation coefficients between the concentrations of the P forms studied in the surface soil layer and total tundra vegetation cover as well as vascular plant and cryptogam cover for the studied transects. The share of tundra vegetation, vascular plant cover, and cryptogam cover for each plot found along the studied

Table 4 Spearman's rank correlation coefficients between different forms of phosphorus and percentage cover of vegetation, vascular plants, and cryptogams in the studied transects combined

Phosphorus form	Vegetation cover	Vascular plants cover	Cryptogam cover
Pl[a]	0.206	0.303*	−0.151
Pml[b]	0.200	0.447*	−0.258
Pst[c]	−0.016	0.366*	−0.061
Ptot[d]	0.136	0.531*	−0.198

*Significant at $p < 0.05$

[a] Labile P

[b] Moderately labile P

[c] Stable P

[d] Total P

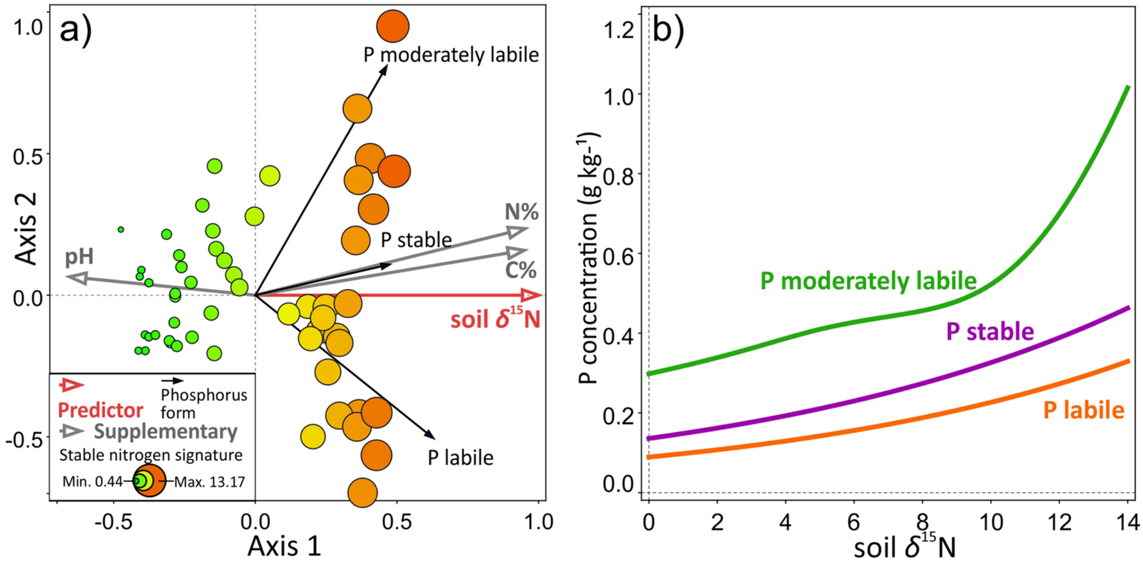


Fig. 5 Impact of soil nitrogen stable isotope ($\delta^{15}N$) on the concentration of the studied phosphorus forms in soil presented as a redundancy ordination plot (RDA) (**a**), and the response of the phosphorus forms presented as generalized additive models (GAMs) (**b**)

transects is listed in the Online Resource 1, Table S1. The percentage share of vascular plants found along all combined transects studied was significantly and positively correlated with the Pl, Pml, Pst, and Ptot contents in the soil. The percentage share of total tundra vegetation and cryptogam cover was not significantly correlated with Ptot and the forms of P studied found in the soil (Table 4).

The concentrations of the studied P forms in the soil significantly explained the composition of the plant species (CCA, pseudo-$F = 3.6$, $p = 0.001$) and also exhibited a very high efficiency equaling 58.4% (Fig. 6a). For vegetation, the most important form of P was found to be Pml (pseudo-$F = 5.1$, $p = 0.003$), which was responsible for 29.7% of the non-random variation noted, followed by the Pl form (pseudo-$F = 3.7$, $p = 0.003$) with a efficiency of 20.6% (Fig. 6a). Stable P did not significantly affect the composition of plant species (pseudo-$F = 1.5$, $p = 0.124$).

Based on a *t*-value biplot with Van Dobben circles, we found that both the Pml and Pl forms affected different sets of species (Fig. 6b). Moderately labile P significantly favored 6 out of 39 plant species, i.e., *Cerastium arcticum*, *Chrysosplenium tetrandrum*, *Deschampsia alpina*, *Saxifraga hyperborea*, *Phipsia algida*, *Cochlearia groenlandica*, and an alga *Prasiola crispa*, while the Pl form favored the

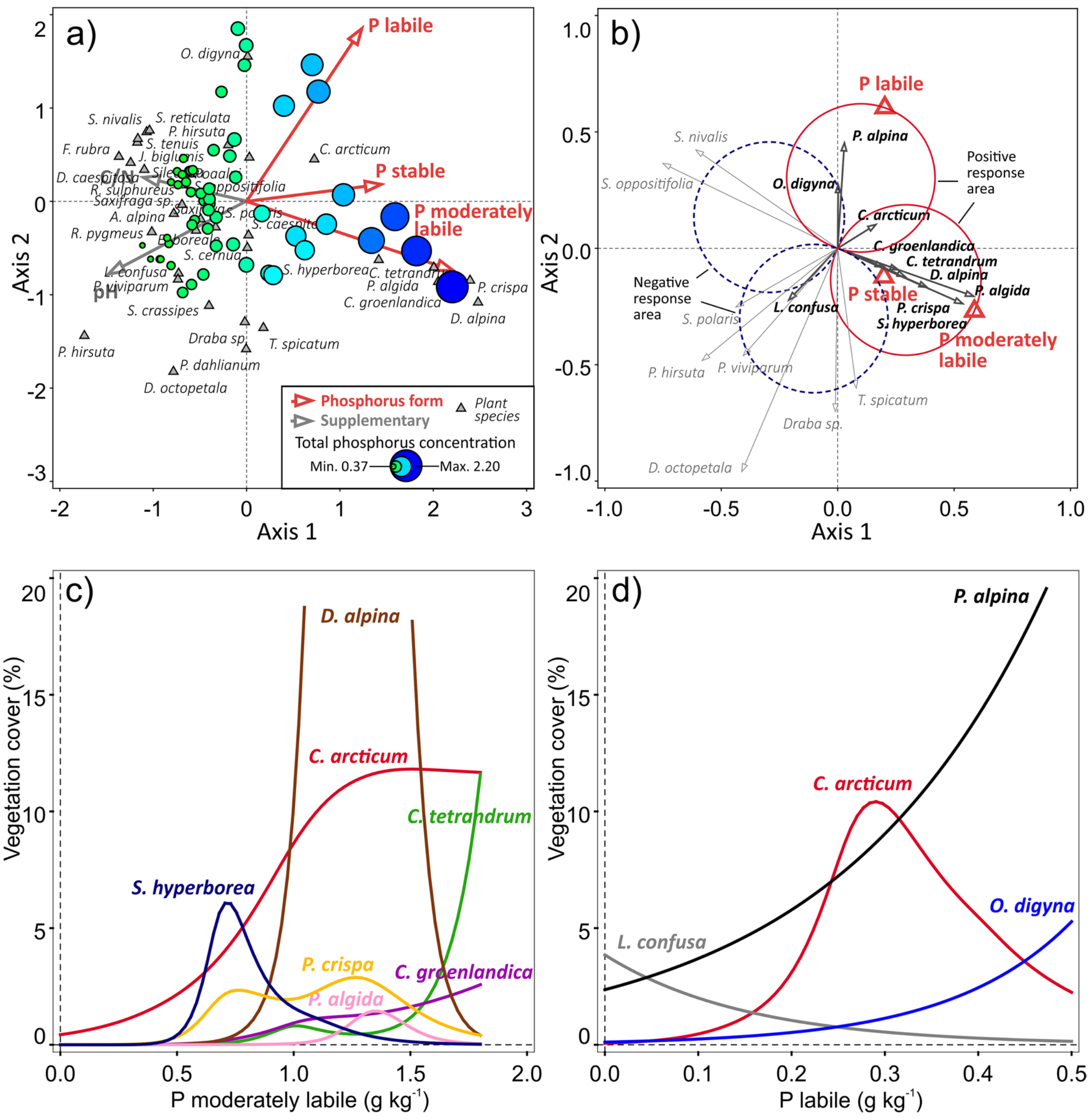


Fig. 6 Impact of the three studied phosphorus forms on the plant species composition presented as CCA diagram showing ordination of plant species and samples (**a**), *t*-value Van Dobben circles showing significant positive and negative species responses to the studied phosphorus forms (**b**), response of selected plant species to moderately labile phosphorus form (**c**), and labile phosphorus form (**d**) presented as generalized additive models (GAMs)

occurrence of *Poa alpina*, *Oxyria digyna*, and *C. arcticum* and suppressed *Luzula confusa*. *Cerastium arcticum* was found to be the only species studied favored by both phosphorus forms noted above (Table 5; Fig. 6b).

The percentage of *C. arcticum*, *C. tetrandrum*, and *C. groenlandica* increased strongly with increasing Pml content in the soil, and similar relationships were observed for *P. alpina* and *O. digyna* in response to Pl (GAMs; Table 5; Fig. 6c, d). At the same time, *D. alpina*, *S. hyperborea*, *P. algida*, and *P. crispa* exhibited unimodal responses in relation to Pml; the same pattern held true for *C. arcticum* versus Pl, suggesting that a high concentration of especially Pml, but also Pl may serve as a limiting factor decreasing the abundance of these species. Although *L. confusa* exhibited a negative response in the *t*-value biplot, the GAM used in the study proved it to be insignificant (Table 5; Fig. 6d).

Discussion

Seabirds are a very important element of the natural Arctic environment and are responsible for the transport of mineral and organic matter from the sea to the terrestrial ecosystem (Godzik 1991; Headley 1996; Zmudczyńska et al. 2012; Zwolicki et al. 2013, 2016a, b; Ziółek and Melke 2014). Based on the relationship between δ^{15}N and the forms of P in the soil, our study strongly suggests that seabirds are locally the most important source of phosphorus in the terrestrial Arctic ecosystem, which substantially affects the composition of vascular plants.

Table 5 Results of generalized additive models (GAMs) of relation between stable nitrogen signature and concentration of the three studied phosphorus forms, and response of selected plant species to the concentration of moderately labile and labile phosphorus forms

Predictor	Response	Model	R^2 [%]	*F*	*p*
δ^{15}N	Pl[a]	lin	39.5	35.1	< 0.001
	Pml[b]	s2	35.7	14.2	< 0.001
	Pst[c]	lin	25.5	16.9	< 0.001
Pml	*D. alpina*	s3	80.3	75.2	< 0.001
	C. tetrandrum	s3	78.5	37.3	< 0.001
	C. groenlandica	s3	76.5	44.9	< 0.001
	P. algida	s3	74.7	37.7	< 0.001
	S. hyperborea	s3	56.2	18.7	< 0.001
	P. crispa	s3	51.9	11.9	< 0.001
	C. arcticum	s2	34.2	9.2	< 0.001
Pl	*C. arcticum*	s3	42.3	10.9	< 0.001
	O. digyna	lin	27.9	9.3	0.003
	L. confusa	lin	13.0	3.8	0.058
	P. alpina	lin	12.6	5.5	0.022

[a] Labile P

[b] Moderately labile P

[c] Stable P

The results obtained in this study indicate that the surface layer of soils that occur along all the studied seabird-affected transects is characterized by a significantly higher mean concentration of Ptot in comparison with soils obtained from all the unaffected transects (Table 1). This finding is related to the deposition of guano, feathers, eggshells, and other biological waste containing P in the nesting area and its vicinity (Stempniewicz 1992; Zmudczyńska et al. 2012; Zwolicki et al. 2013). Stempniewicz (1990) states that during the breeding season, little auks are able to supply up to 60 t km^{-2} of dry fecal matter in the vicinity of their breeding colony in the Hornsund area. Zwolicki et al. (2013) were able to show that the daily guano deposition rate in the center of the little auk colony in the Hornsund area reaches 1.2 g m^{-2}. In addition, a previous study has clearly shown that guano deposition near the little auk colony in the Hornsund area is significantly greater than in areas unaffected by the studied seabirds (Zwolicki et al. 2013). Therefore, the concentration of Ptot, Pl, Pml, and Pst in soils obtained from seabird-affected transects is generally higher than in unaffected transects (except Pml in the Magdalenefjorden area). The significant and positive correlation coefficients obtained between the δ^{15}N isotopic signature of the soil and the concentration of all forms of P studied in the soil confirm that the concentration of P in the soil is strongly related to seabird fertilization, because soils fertilized with guano of little auks were shown to be characterized by substantially higher content of the δ^{15}N in relation to soils not fertilized with guano of these birds (Skrzypek et al. 2015; Zwolicki et al. 2016b; González-Bergonzoni et al. 2017; Wetterich et al. 2019).

The results obtained in this study are generally in agreement with the results presented by Ziółek and Melke (2014) for a black-legged kittiwake bird colony (*Rissa tridactyla*) in the Bellsund area (Wedel Jarlsberg Land, western Spitsbergen), Otero et al. (2015) for seagull colonies (*Larus michahellis*) in the Atlantic Islands National Park (NW Spain), Simas et al. (2007) for penguin rookeries in King George Island, Maritime Antarctica, and Breuning-Madsen et al. (2008) for great cormorant (*Phalacrocorax carbo sinensis*) colonies in Denmark. They also observed clearly higher concentrations of Ptot and different forms of P in soils at sites located in the vicinity of the birds colony in comparison with sites unaffected by the birds (Simas et al. 2007; Breuning-Madsen et al. 2008; Ziółek and Melke 2014; Otero et al. 2015). However, soils affected by black-legged kittiwakes and penguins are characterized by clearly higher concentrations of Ptot and different forms of P in comparison with soils affected by little auks (Simas et al. 2007; Ziółek and Melke 2014). On the other hand, soils affected by seagulls show a lower or similar Ptot concentration in comparison with soils affected by little auks (Otero et al. 2015). Comparison of different forms of P between our study and the study of Breuning-Madsen et al. (2008) and Otero et al. (2015) was not possible due to the different protocols used for P fractionation. The differences obtained in the concentration of Ptot and different forms of P between our study and the studies provided by Simas et al. (2007) and by Ziółek and Melke (2014) are most likely linked with differences in the diet and body size of seabirds between the different bird species. The little auk is a planktivorous species feeding mainly on copepods (*Calanus glacialis*, *Calanus hyperboreus*, *Calanus finmarchicus*) (Stempniewicz 2001; Jakubas et al. 2007), and its guano contains markedly lower amounts of phosphate than that of penguins, which feed mainly on Antarctic krill (*Euphausia superba*) and black-legged kittiwakes, which feed primarily on polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) (Andersson et al. 1988; Brekke and Gabrielsen 1994; Mehlum et al. 1998; Mehlum 2001; Zwolicki et al. 2013; Grzesiak et al. 2020). Furthermore, little auks, kittiwakes, and especially penguins differ in body mass (Brekke and Gabrielsen 1994; Gaston and Jones 1998; Stempniewicz 2001; Strøm, 2005; Halsey et al. 2008), and therefore kittiwakes and penguins surely produce more amount of guano per day than little auks. The next reason for differences in concentration of Ptot and different forms of P in soils affected by these different seabird species is the shorter nesting period of little auks versus kittiwakes and penguins (Brekke and Gabrielsen 1994; Gaston and Jones 1998; Kemp and Dann 2001; Stempniewicz 2001; Strøm 2005; Zwolicki et al. 2013), as well as the fact that kittiwakes and penguins spend more time inside the breeding colony relative to little auks, which are characterized by frequent circling around and over the breeding colony (Stempniewicz et al. 2007; Zwolicki et al. 2013). The behavioral characteristics mentioned above of the little auks could be responsible for much lower concentrations of guano in the breeding area than in the case of kittiwakes and penguins. It should also be noted that the number of birds in the colony is also one of the crucial factors that affects the concentration of P in the soil. The concentration of Ptot and that of different forms of P in the surface soil layer studied indicates that the impact of planktivorous seabirds on soils is clearly weaker than the impact of penguins (Simas et al. 2007) and piscivorous seabirds (e.g., black-legged kittiwake) (Ziółek and Melke 2014). This is also in agreement with the results presented by Zwolicki et al. (2013), who compared the impact of piscivorous and planktivorous bird species in the Hornsund area on the chemical properties of soils such as pH, concentration of NH_4^+, NO_3^-, K^+, and PO_4^{3-}. The study indicates that the concentration of PO_4^{3-} ion in soils affected by piscivorous seabirds such as Brunnich's guillemot and black-legged kittiwake is 17 times higher than in soils affected by planktivorous little auks (Zwolicki et al. 2013). This is related to a clearly higher phosphate content in fish tissues than in zooplankton (Andersson et al. 1988).

The biogeochemistry of P in soil is very complex and results from a variety of dynamic processes such as mineralization, sorption, desorption, dissolution, immobilization, and plant uptake (Frossard et al. 1995; Shen et al. 2011; Niederberger et al. 2017). Furthermore, the complex biochemical relationships observed between inorganic, organic, and microbial forms of P have a strong impact on the concentration of individual forms of P in the soil (Condron and Newman 2011). The higher concentration of Ptot and all the forms of P studied (but not always significantly higher) found in soils occurring along seabird-affected transects in comparison with soils from unaffected transects is likely also related to the significantly higher content of organic matter in the former soils (with the exception of the Isfjorden area). It has been shown that soils containing a high content of organic matter exhibit a higher ability to absorb P than soils with a low organic matter content (Craft and Richardson 1993; Wang et al. 2012; Ziółek and Melke 2014). This finding is confirmed by the significant and positive correlation coefficients observed for the concentration of Ptot and all forms of P studied and the TOC content in the soils studied (Table 3). The prevalence of moderately labile P and especially the part of Pml extracted using NaOH in the studied soils (see Online Resource 1, Table S1) indicates that the majority of P in these soils is P bound to organic matter and/or organo-mineral complexes featuring Al and Fe oxides (Simas et al. 2007; De La Peña-Lastra 2021). This is mainly related to the high mean organic matter content and the acidic or slightly acidic pH of the soils studied, as the concentration of different P forms in the soil depends on the soil pH (Ann et al. 2000; Brady and Weil 2004; Ziółek and Melke 2014; De La Peña-Lastra 2021). In soils exhibiting low pH, P is fixed mainly by soluble Fe and Al and/or amorphous Fe and Al oxides and oxyhydroxides, while in neutral and alkaline soils, P is bound mainly by Ca that forms calcium phosphate (Brady and Weil 2004; Ziółek and Melke 2014; De La Peña-Lastra 2021). Ziółek and Melke (2014) indicated that the labile P form is supplied directly to the soil by seabird deposition of guano. This is a very important input of P to the nutrient-poor terrestrial High Arctic environment, which is responsible for the primary succession of plants to these fertilized sites and the better development of vegetation cover than at sites unaffected by seabirds. This labile P form may be easily absorbed by plants, and following the death of the entire plant or at least its above- or belowground parts, this P form returns to the soil as organic residue enriched in P. Therefore, the moderately labile pool of P, which is partially bound to organic matter and prevails in the soils studied, exhibits a significantly higher concentration in soils fertilized by little auks compared to soils unaffected by birds (with the exception of the Magdalenefjorden area). The better developed vegetation cover and the higher supply of organic matter in soils occurring at sites fertilized by little auks versus other sites may also be responsible for the higher concentration of the stable form of P in soils affected by birds versus soils from unaffected transects. It has been shown that the availability of the labile form of P in the soil may become restricted due to occlusion in poorly decomposable organic compounds (Walker and Syers 1976).

The results of our study indicate that the concentration of Ptot and P forms is highly different at each study site (Table 1; Figs. 3, 4). The highest mean content of Ptot in soils along the seabird-affected transect in Hornsund is most likely related to the highest number of little auks (i.e., ~ 47,000 individuals) among all the studied sites. On the other hand, the lowest mean Ptot concentration in soils along the seabird-affected transect in the Isfjorden area is related to the lowest number of little auks (i.e., only ~ 500 individuals). The highest mean concentration of Pl in soils located along the seabird-affected transect at Magdalenefjorden site may be related to the high supply of this form of P to the soil through bird droppings and the lower degree of vegetation development (in comparison with Hornsund site; see Online Resource 1, Table S1), which can absorb this form of P. The lowest mean concentration of Pl in soils that occur along the seabird-affected transect at the Isfjorden site is most likely connected with the lowest number of seabirds at this site. The highest mean concentration of Pml in soils located along the seabird-affected transect in Hornsund may be related to the higher content of Fe and Al hydroxides in soils due to the higher degree of weathering, because of the better developed vegetation (see Online Resource 1,Table S1). Szymański et al. (2016a) indicated that the surface soil layers in this area are characterized by a high content of Fe and Al oxides, and these oxides can fix P, forming Pml. The lowest mean concentration of Pml in soils occurring along seabird-affected transect in the Magdalenefjorden area is most likely related to lower content of Fe and Al hydroxides in soils due to lower degree of weathering in comparison with Hornsund and Isfjorden sites, because of the most harsh climate conditions (this site is northernmost among all the studied sites) (Fig. 1). The soils along the seabird-affected transect in the Magdalenefjorden site are characterized by the highest mean concentration of Pst and this form of P prevails over the forms of Pl and Pml (Table 1). This indicates that the highest proportion of P in these soils occurs in the internal structure of minerals (e.g., apatite) and/or is strongly bound to minerals and/or occurs in organic residue. The lowest mean concentration of Pst form in soils located along seabird-affected transect in the Isfjorden site is most likely related to different mineral composition of these soils and/or higher degree of organic matter transformation due to the mildest climate conditions among the studied sites. However, it should be noted that the differences obtained in the concentration of different forms of P between the studied sites and the different trends in the concentration of P forms along each studied transect could also be related to the local heterogeneity of soil types (Szymański et al. 2013) and its properties such as, for example, pH, TOC content (Table S1), mineral and chemical composition (Szymański et al. 2016a, b) as well as the local heterogeneity of plant communities (Zwolicki et al. 2016a). In addition, the local impact of guano and biological waste originating from other animals such as reindeer (*Rangifer tarandus spitzbergensis*) or Arctic fox (*Vulpes lagopus*), as well as the local anthropogenic impact (in the Hornsund and Isfjorden areas) should be taken into account in explaining the concentration of P and its different forms in the soils studied.

The availability of P in the soil is a very important ecological factor responsible for plant growth and abundance, especially in the nutrient-poor High Arctic environment (e.g., Solheim et al. 1996; Robinson 2002; Madan et al. 2007; Chapin and Körner 2013). We found that the gradient of the concentration of P form in the soil generated by seabirds changes vascular plant composition to a great extent and this is in line with our stated hypothesis and the results presented by De La Peña-Lastra et al. (2021) from the northwestern part of Spain. However, it should be noted that the high value of explained variation likely cannot be interpreted as a direct response of plants to local phosphate content or availability, because in seabird-fertilized soils, phosphates are highly positively correlated with other nutrients, i.e., nitrogen and potassium (Zwolicki et al. 2013, 2016b).

The availability of P in the soil is highly dependent on the form of P, and it is well known that the labile pool is generally the main source of P, which is largely responsible for the release of P into the soil solution, from where P is actively taken up by plants (Williams et al. 2013; Niederberger et al. 2017). Our results confirm that the labile P form is very important for plant composition as the most accessible P form for plants, because we have shown that some plant species such as, for instance, *P. alpina* and *O. digyna* positively respond to higher concentration of Pl in the soil (Table 5; Fig. 6d), and this is in agreement with our hypothesis. However, our results indicate that Pml also affects the composition of plant species (Table 5; Fig. 6c). The stable form of P may also be important for plants; however, this is not directly due to the very slow re-release of phosphates into the more labile form and this is most likely why this particular form was insignificant in our model. Furthermore, we found that the cover of the vascular plants is significantly and positively correlated with the concentration of Ptot and all the forms of P studied in the soil (Table 4). On the other hand, no significant relationships were observed between the concentration of Ptot and all the P forms studied found in the soil and total vegetation cover as well as cryptogam cover (Table 4). This finding indicates that, in general, vascular plants respond positively to the influx of P to the soil via seabird guano deposition, whereas cryptogams do not. Most likely, this is connected with the different nutritional strategies of vascular plants and cryptogams. Cryptogams (i.e., bryophytes and lichens) exhibit a limited ability to take up soil nutrients (Pointing et al. 2015; Roos et al. 2019) due to their lack of a typical root system (Longton 1988). Cryptogamic organisms can absorb nutrients from precipitation or atmospheric deposition (Longton 1988; Cornelissen et al. 2007). On the other hand, vascular plants rely mainly on nutrients that occur in the soil. However, we also found that not all species of vascular plants are significantly affected by P fertilization. Furthermore, species such as *C. arcticum*, *P. alpina*, and *O. digyna* are significantly and positively related to labile P found in the soil, while species such as *C. groenlandica*, *C. tetrandrum*, *D. alpina*, *P. algida*, *S. hyperborea*, and *C. arcticum* are significantly and positively related to Pml in the soil. This indicates that some species of vascular plants found in the High Arctic environment are able to use only the most labile fraction of P, while other species may use forms of P less readily available to plants. Given that plant life history decisions are determined by nutrient availability, the ability to quickly adapt to increasing nutrient supplies should give a competitive advantage over species accustomed to low nutrient levels (Hill et al. 2011). The positive response of vascular plants to P fertilization was found in highly competitive species that were frequently found close to bird colonies and are characterized by rapid growth, high fecundity, and rapid tissue turnover (Summerhayes and Elton 1928; Eurola and Hakala 1977; Odasz 1994; Zwolicki et al. 2016a, b).

Conclusions

1. The surface layer of soils affected by planktivorous seabirds (i.e., little auks) is characterized by a significantly higher mean concentration of Ptot in comparison with surface layers unaffected by the birds. Concentration of different P forms is also generally higher in soils affected by the seabirds than in unaffected soils, however, the differences are not always significant.
2. All the P forms studied here are significantly and positively correlated with the concentration of stable nitrogen isotope (δ^{15}N) in the soil, indicating that its origin is connected with seabird-related soil fertilization. Furthermore, the concentration of Ptot and all of the studied P forms in the studied soils is significantly and positively related to the concentration of TOC and TN in the soil.
3. Vascular plant cover is significantly and positively related to the concentration of Ptot and all studied P forms found in the soil. The composition of plant community changes significantly along the phosphorus concentration gradient. Moreover, it was found that moderately labile P, followed by the labile P fraction, are the most important forms of P for plants, promoting the growth of different vascular species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-023-03124-w.

Acknowledgements This study was financially supported by the Faculty of Geography and Geology at Jagiellonian University in Kraków (based on Decision No. DS/MND/WGiG/IGiGP/2018/25) and the Polish Ministry of Science and Higher Education (Grant Nos. 3290/B/P01/2009/36, 1883/P01/2007/32 and IPY/25/2007) as well as the Polish-Norwegian Research Fund (Grant No. PNRF-234-AI-1/07, ALKEKONGE). The authors would like to thank the reviewers for their helpful suggestions. Language editing was done by Grzegorz Zębik.

Author contributions W.S. wrote the main manuscript text, prepared figures 1-4, and tables 1-4. M.S. determined P forms in laboratory and assisted in preparation of the main manuscript text. A.Z. collected soil samples, assisted in preparation of the main manuscript text, prepared figures 5 and 6, and table 5. K.Z.S. collected soil samples, assisted in preparation of the main manuscript text. L.S. assisted in preparation of the main manuscript text. All authors reviewed the manuscript.

Data availability The data generated and analyzed in this study are included as raw data in the supplementary information file.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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